Cloning and Aggression among Sea Anemones (Coelenterata: Actiniaria) of the Rocky Shore

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Abstract. Among the common rocky shore anemones of Pacific North America, New Zealand, and Tropical Australia, clonal growth is significantly correlated with other features of the biology including aggressiveness, habitat, and body size. Individual size is more variable among aclonal species and among species living on the lower shore; and aclonal individuals are larger on average than clonal individuals. Aclonal species are usually non-aggressive inhabitants of the lower shore, while clonal species are usually aggressive residents of the upper shore. To explain the link between cloning and aggression, a geometric model is developed that compares the scaling of interference budgets for isometric aclonal growth, and for two-dimensional growth of a compact, encrusting clone. The ratio of exposed perimeter to feeding surface area (P/S) declines more steeply through clonal spread than through aclonal growth; and therefore, the costs of interference relative to energy intake rates should be *lower* for a short, squat clone than for a single, bulbous individual of the same volume. Association with mutually tolerant individuals can also reduce the *per capita* costs of interference (*The Three Musketeers* effect—a special case of the geometric model). Cloning may be more common among anemones living higher on the shore because clonal individuals are generally smaller than their aclonal counterparts, and because predators that prefer small anemones tend to be more abundant downshore.

Introduction

Because they are very different from the kinds of animals usually described as aggressive, the sea anemones (Class: Anthozoa, Order: Actiniaria) provide a potentially useful source of comparative information on the

ecology and evolution of intraspecific interference behaviors, and on the evolution of social aggression, which involves both interference and cooperation.

Anemones from rocky shores are soft-bodied, attached, and weakly mobile carnivores that may also derive part of their nourishment from intracellular algae. In addition to growing in a conventional manner when fed, anemones shrink or degrow when undernourished. Some also replicate asexually to form clones of autonomous and mobile individuals; and for these, the maximum size of the clone may be very large, even when individual size is quite small. Furthermore, there is no evidence that anemones necessarily deteriorate with age, though of course many die of natural causes other than senescence (Shick *et al.*, 1979). Consequently, ordinary words like *individual, size, age,* and *growth* can become disconcertingly slippery when applied to the anemones.

Defined for my purposes here, an *individual* (= ramet *sensu* Harper, 1977) is the temporarily distinguishable physical/physiological entity, *i.e.*, a single anemone with a pedal disc for attachment to the substratum, a single opening to the gut for ingestion and egestion, and a set of tentacles surrounding the mouth and oral disc. A *clone* (= genet, *sensu* Harper, 1977) is all of the genetically identical individuals derived from a single zygote by asexual replication. And a *colony* is a group that retains functional connections among the clone members, generally called *polyps* (= modules, *sensu* Harper, 1977).

Aggression is defined conventionally as specialized and directed behavior in which an individual inflicts or attempts to inflict damage on another individual. This is the most active and dramatic form of *interference competition,* which is an activity that's advantage is derived indirectly from its direct cost to a competitor. By contrast, *exploitation competition* is usually understood to be use or monopoly of a resource, an activity that adversely

effects competitors only incidentally, by limiting their access to resources. *Social aggression* is defined here as active, directed, and more or less coordinated interference between groups of individuals belonging to the same species. While *competition* results in net cost to both parties, *cooperation* is an interaction that results in mutual benefit.

Specialized interference behaviors are known to have evolved only twice among the anemones (Williams, 1975). Some acontiate anemones form long, specialized catch-tentacles that bear large, holotrich nematocysts in place of the nematocyst complement typically found in feeding tentacles (Williams, 1975; Purcell, 1977; Watson and Mariscal, 1983). When these anemones touch a genetically different conspecific (or any other member of the class Anthozoa), one or more of the catch-tentacles expands, extends, and probes the surrounding area. On touching the body of a competitor, the tip adheres and breaks loose from the rest of the tentacle. Some actiniid anemones attack each other using acrorhagi, blunt structures at the top of the column beneath the outer cycle of tentacles (Äbel, 1954; Bonnin, 1964; Francis, 1973b; Bigger, 1976; Brace and Pavey, 1978; Ottaway, 1978; Brace, 1981; Ayre, 1982; Sebens, 1984; Fujii, 1987). When their tentacles touch a genetically different anthozoan, these anemones inflate the adjacent acrorhagi. With stretching and bending movements of the oral disc and column, they wipe these turgid structures against the adversary, leaving large scraps of adhering ectodermal tissue. Firing of the numerous large holotrich nematocysts in the adhering tissue from an acrorhagus or catch-tentacle damages the victim.

These behaviors are specific (Bonnin, 1964; Francis, 1973b; Williams, 1975; Bigger, 1976, 1980; Lubbock, 1980), inducible (Francis, 1976; Purcell, 1977; Watson and Mariscal, 1983) and costly (Francis, 1976). The acrorhagial and catch-tentacle responses serve no apparent functions in feeding or defense against predators, but are elicited only in response to contact with potential competitors belonging to the same or related species. The anemones respond aggressively to contact with genetically different members of their own and other anthozoan species, but passively tolerate contact with genetically identical tissue (their own or that of a clonemate). The specialized weaponry is inducible, so individuals can vary their investment in aggression in response to the particular circumstances.

Isolated individuals and those living in the middle of segregated clones have little or no fighting equipment, while those living in contact with genetically different individuals develop more and larger weaponry and show greatly reduced investment in sexual reproduction. As a further refinement, individuals of some species attack a new neighbor very readily, but are more tolerant of contact with long-term neighbors (Purcell and Kitting, 1982; Sebens, 1984); and some apparently attack only nonclonemates of the same sex (Kaplan, 1983).

Some species of anemones are aggressive and some are not. Since even within aggressive species individuals that are not in contact with competitors apparently reduce or lose their fighting equipment (Hand, 1955b; Williams, 1975; Francis, 1976; Purcell, 1977; Watson and Mariscal, 1983), catch-tentacles and acrorhagi are not likely to become vestigial. I would argue that whatever initially favored the evolution of these inducible interference behaviors, selection must still favor the production, use, and maintenance of this specialized equipment. Of course, the converse is not necessarily true; species living in circumstances favoring the evolution of aggressive behaviors may simply never have developed them. Nonetheless, on average we might expect to find differences in the biology and the ecology of aggressive species, as compared with non-aggressive ones. Data are presented here on the interaction of aggression, individual body size, cloning, and position on the shore; and a simple geometric model is developed to explain the strong correlation between cloning and aggression.

Materials and Methods

Selection of the sample

The sample includes common or locally abundant species from exposed to semiprotected rocky areas where I have worked over the past ten years. Rare species were excluded for consistency, because they were likely to be overlooked in areas where the anemone fauna is not as well described (Southeast Alaska, Baja California, and tropical Australia). Because encounters between members of rare species will generally be uncommon, intraspecific interference presumably will also be uncommon; and eliminating rare species from the sample should simply sharpen the focus of the present study.

Observation and handling of specimens

In little studied areas, I talked with local naturalists, visited accessible rocky sites, and examined the open rocks, crevices, overhangs, and pools at low tide. Each species was observed in the field and, whenever possible, a few individuals were also collected and observed in the laboratory. Specimens of unidentified species were anesthetized with magnesium sulphate (Francis, 1976); squashes of tentacles, and of spherules, warts, and knobs on the upper column were examined microscopically for holotrichs. Anesthetized animals were then preserved in formalin, and those from Mexico and Alaska were later sent to D. Fautin (California Academy of Sciences) for identification.

Study sites

The study areas include two long north-south gradients extending from subarctic to subtropical latitudes, plus a tropical shore. Observations were made and new information is reported (*) from the following sites (arranged north-to-south) along the Pacific Coast of North America: (1) *Torch Bay, Alaska (58°20′ N, 136°05′ W), (2) San Juan Island, Washington (48°28′ N, 123°03′ W), (3) Newport, Oregon (44°40′ N, 124°04′ W), (4) Santa Cruz, California (36°57′ N, 122°04′ W), (5) Gaviota, California (34°27′ N, 120°04′ W), (6) La Jolla, California (32°52′ N, 117°16′ W), (7) *Punta Banda, Baja California, Mexico (MX$_1$ = 31°44′ N, 116°43′ W), (8) *San Quentin, Baja California (MX$_2$ = 30°23′ N, 116° W), (9) *Punta San Juanico, Baja California (MX$_3$ = 26°12′ N, 112°20′ W), (10) *Punta Conejo, Baja California (MX$_4$ = 24°17′ N, 11°22′ W), and (11) *San Jose del Cabo, Baja California (MX$_5$ = 23°N, 109°42′ W). Field sites in New Zealand (arranged north-to-south) include beaches on both the east and west coasts of the North Island and the South Island: (1) Leigh, North Island (36°17′ S, 174°48′ E), (2) Muriwai Beach (36°50′ S, 174°25′ E), (3) Abel Tasman, South Island (41°S, 173°E), (4) Kaikura (42°26′ S, 173°44′ E), (5) Okarito (43°14′ S, 170°09′ E), and (6) Portobello (45°51′S, 170°40′ E). Rocky intertidal sites were also examined in North Queensland, Australia: (1) *Lizard Island (AU$_1$ = 14°69′ S, 145°45′ E), (2) Cape Tribulation (16°04′ S, 145°29′ E), (3) Magnetic Island (19°10′ S, 145°50′ E), and (3) Australia Institute of Marine Science, nr. Townesville (19°15′ S, 147° E).

Assignment to categories

The habitat was categorized either as upper shore (the high and mid-intertidal, extending down to include the zone usually occupied by mussel beds on temperate shores), or as lower shore (the intertidal below mean low tide, and the shallow subtidal just below the lowest tidal excursions).

Sizes reported are individual body size (column diameter in centimeters) for individuals at the upper end of the average reported size range (Parry, 1951, 1952; Hand 1955a, b; Dunn *et al.,* 1980; Bucklin and Hedgecock, 1982; Fautin and Chia, 1986). This was not a search for very large individuals, but rather an estimate of how large individuals ordinarily become.

Species categorized as clonal are those directly observed to fragment, those showing indirect evidence of fragmentation (fission scars), those reported to brood genetically identical offspring, and (tentatively, for species whose growth and reproductive patterns are not well studied) color-variable species occurring in aggregations that are segregated by color-type.

Species were classified as aggressive if even one individual was found with acrorhagi or catch-tentacles. Since these structures are inducible and used only in interference competition, it seems justifiable to use even a single occurrence as diagnostic. Species never observed to produce either catch-tentacles or acrorhagi are tentatively categorized as non-aggressive.

Statistical treatment

A multi-way G-test was used to determine the significance level for shore position, clonal/aclonal growth, and aggressiveness, acting simultaneously. In addition, since some of the theoretically possible sets are empty, it is permissible, if conservative, to use Fisher's exact test with critical alpha levels corrected to compensate for multiple use of data [comparisonwise error rate = $1 - (1 - \text{alpha})^{1/c}$, where c is the number of comparisons and alpha is the desired level of confidence; Sidak, 1967, cited in SAS guide, 1985]. (For three sets of comparisons, a comparisonwise error rate of 0.0165 is equivalent to an experimental error rate of 0.05.)

Development of a model

A geometric model is developed that predicts the relative energy efficiency of interference as a function of increasing size: (1) for growth through isometric increase in size (simulated growth of an aclonal adult), and (2) for growth without increasing in height (simulated growth and spread of a compact, encrusting clone).

Results

Correlations

The individual species included in the sample, together with information on geographic location, shore position, individual size, aggressiveness and mode of growth, are shown in Table I. Simultaneous and pairwise interactions of clonal growth, shore position and aggressiveness are shown in Figure 1 (a three dimensional $2 \times 2 \times 2$ table, projected onto three 2×2 tables). Data on individual size are shown superimposed on the same three dimensional matrix (Fig. 2).

Overall, species are not evenly distributed with respect to shore position, clonal/aclonal growth and aggressiveness (Fig. 1) (G-test using a log-linear model with a three-way table, $P \ll .001$). Tested separately, two of the three pairwise interactions are significant (for cloning *vs.* aggression and for cloning *vs.* shore position, $P < .05$ for experiment-wise error rates). Clonal species are more commonly aggressive while aclonal species are more often not aggressive; and clonal species tend to live on the upper shore, while aclonal species are more often found on the lower shore. Using the Fisher's Exact Test (two tailed), comparisonwise error rates are 0.00023 (for

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Table I

Individual size, habitat, and habits of common shore anemones from the rocky intertidal of Pacific North America, New Zealand, and tropical Australia, arranged by tidal height

Species[**]	Clonal	Aggressive	Upper shore[2]	Individual size[3]	Geographic location[4]	Information source[1]
Anthopleura aureoradiata	+?*	+	+*	2	AU, NZ	h, *
Isactinia olivacea	+?*	−	+	3.5	NZ	h, *
Anthopleura sp. 1	+	+	+	1	MX$_{3-5}$	*
Haliplanella lineata (luciae)	+	+	+	2	US	e
Actinia tenebrosa	+	+	+	3*	AU, NZ	h, *
Anthopleura elegantissima (clonal form)	+	+	+	3	AK, US, MX$_{1-4}$*	e*
Cnidopus veratra	+?*	+	+	2.5	AU, NZ	g, *
Anthopleura? sp. 2	+	+	+	3	AU$_1$	*
Phymactis papillosa	+	+	+	3	MX$_4$	*
Aiptasia? sp.	+	−	+	0.5	MX$_5$	*
Phymanthus sp.	−	−	+	5	MX$_5$	*
Phymanthus muscosus	−	−	+	3	AU$_1$	*
Oulactis muscosa	+?*	+	+	4	AU, NZ	h, *
unidentified	+?	−	+	2	AU$_1$	*
Aulactinea incubans	−?	−	+	2.5	US	b
Epiactis thompsoni	−?	−?	0	5	NZ	h
Epiactis prolifera	−	−?	0	4	US	f
Epiactis fernaldi	−?	−?	0	2.5	AK*, US	c, *
Epiactis sp. 1	−?	−?	0	3	AK	*
Epiactis sp. 2	−?	−?	0	3	AK	*
Isocradactis magna	−	+?	0	9	NZ	h
Anthopleura minima	+	+	0	1.5	NZ	h
Anthopleura xanthogrammica	−	+	0	20*	AK, US, MX$_1$*	f, *
Actinodendron sp.	−	−	0	4	AU$_1$	*
Epiactis (Cnidopus) ritteri	−	−	0	5	US	f
Anthopleura elegantissimi (solitary form)	−d	+	0, −*	20*	US, MX$_{1-2}$*	d, f, *
Anthopleura artemisia	+?*	+	0, −*	4	US, AK*	f, *
Metridium senile	+	+	0, −	4	US	e
Urticina (Tealia) crassicornis	−	−	0, −	9	US	f
Urticina (Tealia) coriacea	−	−	−	9	US	f
Actinothoe albocincta	−?	−	−	0.8	AU, NZ	i
Urticina (Tealia) lofotensis	−	−	−	9	US	f
Cricophorus nutrix	−?	−	−	1.5	AU, NZ	i
Phlyctenactis tuberculosa	−	−	−	10	AU, NZ	h
Metridium sp.	−	−	−	10	US, AK	a

[1] = Sources of information: (a) Bucklin and Hedgecock, 1982; (b) Dunn *et al.*, 1980; (c) Fautin and Chia, 1986; (d) Francis, 1979; (e) Hand, 1955a; (f) Hand, 1955b; (g) Ottaway, 1975; (h) Parry, 1951; (i) Parry, 1952; (*) new observation.

[2] = Upper shore animals (+) living at or above the lower mid-tide level; lower shore anemones living near the low water mark (0) and in the shallow subtidal (−).

[3] = Column diameters measured in centimeters for animals at the upper end of reported normal size ranges.

[4] = Glacier Bay, Alaska (AK), Queensland, Australia (AU), Baja California, Mexico (MX), Continental United States, Pacific Coast (US), New Zealand (NZ). Numbers indicate specific sites listed in the text.

[**] = Species ordered by tidal height, beginning at the top of the shore and working down to the shallow subtidal.

? = Designation tentative.

clonal growth *vs.* aggression and for clonal growth *vs.* shore position), and 0.27 (for aggression *vs.* position on the shore). While it would be desirable to determine whether the factors acting in pairs are effective for a given condition (*e.g.*, the interaction of cloning and aggression within a habitat [upper shore or lower shore]), the samples are not yet large enough to allow meaningful testing.

Overall, the data on individual size (Fig. 2) are not evenly distributed with respect to clonal/aclonal growth (F-test using a linear model, 3-way ANOVA; $P < .05$ both for raw data and for log-transformed data). Clonal species tend to be smaller than aclonal species. Bartlett's test for homogeneity of variance also indicates that the variances are not evenly distributed ($P < .05$). Aclonal species are more variable in body size than clonal species; and those living on the lower shore are more variable
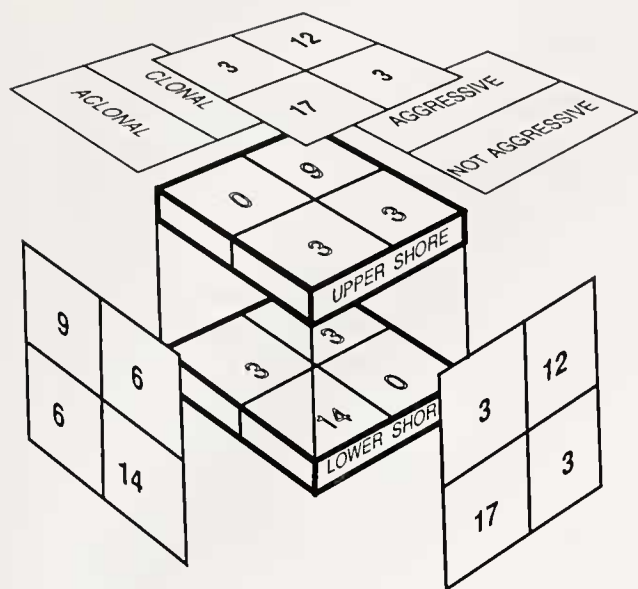
Figure 1. Numbers of common anemone species from the rocky shores of Pacific North America, New Zealand and tropical Australia, grouped by habitat (upper shore or lower shore), intraspecific aggressiveness (aggressive or non-aggressive), and mode of growth (clonal or aclonal). The $2 \times 2 \times 2$ table shows simultaneous interaction among the three factors for the 35 species (center); and the three 2×2 tables show interactions for two factors at a time [clonal growth pattern vs. aggression (above), clonal growth vs. shore position (right), and shore position vs. aggression (left)].

than those on the upper shore ($P < .05$). The sample is not large enough to reveal any differences between individual cells in the $2 \times 2 \times 2$ table except the most extreme: high, clonal aggressive species are smaller on average than low, aclonal, non-aggressive species, (Tukey-Kramer method for multiple comparisons, $P < .05$ for the experimentwise error rate).

An energy efficiency model: the scaling of interference costs for clonal and aclonal growth

Both the rate of encounter with competitors and the rate of energy intake should vary with the size and shape of the individual, and with the size and shape of the clone (for clonal species). The model developed below predicts the scaling of interference cost as a fraction of the total energy intake for isometric aclonal growth, and for two dimensional growth of a compact clone.

The assumptions of the model are as follows: (1) aclonal growth is assumed to be isometric (no change in shape), as it is for at least some anemone adults (Sebens, 1981). (2) Clones are assumed to form a compact sheet of equal-sized individuals that are attached to the substratum at the base, and that use the upper surface (S) for feeding. (3) Energy intake rate is assumed to increase in direct proportion to the feeding surface area, (Sebens,

1981, 1982a). (4) The rate of contact with competitors, and therefore the rate of expenditure for interference (including cost for making and maintaining fighting equipment, for fighting, and for wound healing), is assumed to increase in direct proportion to the length of the external perimeter (P). (5) Therefore, the fraction of energy intake devoted to interference should be directly proportional to the ratio of exposed perimeter to surface area (P/S).

The basic geometric relationships derived from these assumptions are summarized in equations 1 through 6. For an aclonal individual, the length of the perimeter (P_i) is directly proportional to individual length (L), or to individual volume (V_i) to the 1/3 power.

$$P_i \propto L \propto V_i^{0.33} \tag{1}$$

Individual feeding surface area (S_i) is proportional to the square of a linear dimension (or individual volume to the 2/3 power).

$$S_i \propto L^2 \propto V_i^{0.67} \tag{2}$$

Therefore, the ratio of individual perimeter to individual surface area is inversely proportional to length (or individual volume to the 1/3 power).

$$P_i/S_i \propto L^{-1} \propto V_i^{-0.33} \tag{3}$$

For a compact, clonal sheet, the length of the external perimeter (P_c) is directly proportional to individual length (or individual volume to the 1/3 power), and to the square root of the number of individuals in the clone (n).

$$P_c \propto L \cdot n^{0.5} \propto V_i^{0.33} \cdot n^{0.5} \tag{4}$$

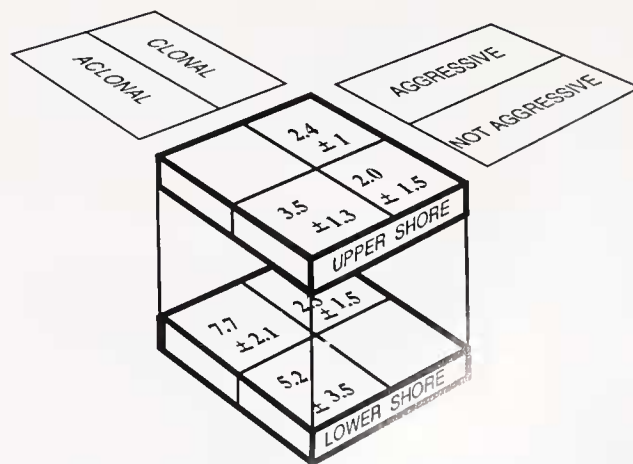Clonal feeding surface area (the upper surface = S_c) is

Figure 2. Individual body size as a function of habitat, aggressiveness and clonal growth for 35 species of rocky shore anemones. Figures given are mean column diameter (in centimeters) for individuals at the upper end of reported, average size ranges, plus or minus one standard deviation.
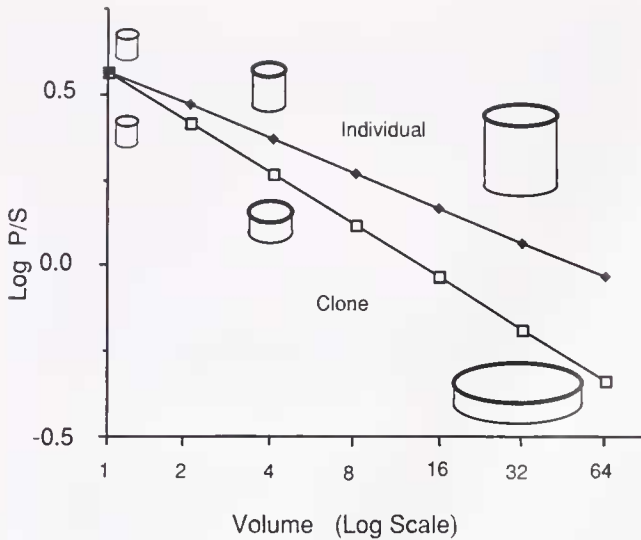
Figure 3. Change in the ratio of external perimeter to upper surface area (P/S) with increasing volume. A. The upper line [$P_i/S_i = 3.69\ V_i^{-0.33}$] shows the decline in P/S with increasing volume for a cylinder that "grows" isometrically, as aclonal anemones do. The following basic, geometric relationships were used in the calculations: L = height = diameter; S_i = upper surface area = $\pi/4 \cdot L^2 = 0.79\ L^2$; P_i = perimeter = $\pi\ L$; $P_i/S_i = 4/L$; V_i = volume = $\pi/4 \cdot L^3$. B. The lower line [$P_c/S_c = 3.69\ V_c^{-0.5}$] shows the decline in P/S for "growth" of a compact, sheet-like clone, modeled as a cylinder that increases in diameter, but not in height. Geometric relationships are as follows: L = height = 1.08; S_c = upper surface area = $n \cdot S_i = \pi/4\ n \cdot L^2$; P_c = perimeter = $\pi\ L \cdot n^{0.5}$; $P_c/S_c = 4\ L^{-1} \cdot n^{-0.5}$; V_c = volume = $V_i \cdot n = \pi/4\ L^3 \cdot n$.

directly proportional to the square of individual length (or individual volume to the ⅔ power) times the number of individuals in the clone.

$$S_c \propto L^2 \cdot n \propto V_i^{0.67} \cdot n \qquad (5)$$

The ratio of clone perimeter to clone surface area is inversely proportional to individual length (or individual volume to the ⅓ power) times the square root of the number of individuals.

$$P_c/S_c \propto L^{-1} \cdot n^{-0.5} \propto V_i^{-0.33} \cdot n^{-0.5} \qquad (6)$$

Predicted differences in the costs of interference relative to energy intake rate are illustrated (Fig. 3) using data for hypothetical cylindrical "anemones" that form short, compact, cylindrical clones. For simplicity, the individual volume of clone members is set equal to one; and clone volume is therefore equal to the number of individuals in the clone (n). Clone feeding surface is also assumed to equal the summed upper surfaces of all clone members [$S_c = n(S_i)$]. Although rigid cylinders cannot be close-packed in this way, the distortions in individual shape necessary to form a compact, cylindrical clone are actually perfectly possible for the protean anemones.

Discussion

Among anemones of the rocky intertidal, the clonal mode of growth is strongly correlated with other important characters including body size, habitat, and aggressiveness. Clonal species tend to be aggressive and to live on the upper shore, while aclonal forms tend to be non-aggressive and to live low on the shore. Twenty-three of the 35 species sampled belong to one or the other of these categories (Fig. 1). *None* are simultaneously clonal, non-aggressive and inhabitants of the lower shore. *None* are aclonal, aggressive inhabitants of the upper shore. This is a very striking pattern that demands explanation.

There are many different methods of asexual replication among the anemones including budding, longitudinal fission, bilateral fission, various kinds of unequal fragmentation (Chia, 1976), and internal brooding of genetically identical young (Black and Johnson, 1979). This suggests that cloning has arisen repeatedly within this group. Further, since clonal and aclonal forms occur within the same genus, and possibly even within the same species (Smith and Potts, 1987; A. Bucklin, pers. comm.), asexual replication may be a relatively labile character that is readily suppressed, as well as repeatedly invented, among the anemones. Therefore, I would argue that the strong correlations between cloning and body size, habitat, and aggressiveness, are ecologically and functionally significant (read "adaptive"), rather than merely historic accidents.

Thoughts on causation: genet size and shape, and the link between cloning and aggression

The geometric model developed here demonstrates the *direction*, not the magnitude, of expected differences in the energy efficiency of interference as a function of size for two different genet shapes.

Where circumstances allow it, growth by cloning should be more advantageous for aggressive species than growth by increase in individual size because the *proportion* of the total energy budget required for interference should be lower for a compact clone than for a large aclonal individual of the same volume ($P_c/S_c < P_i/S_i$, Fig. 3). While increase either in individual size or clone size reduces the ratio P/S, Sebens (1981) has shown that the feeding surface area of anemones increases as a lower power function (of individual weight or volume) than does metabolic rate. Continued increase in *individual* body size beyond the energetic optimum for the particular conditions therefore will result in a progressively lower energy surplus above maintenance level metabolic costs, which eventually will preclude reproduction as well as interference. By contrast, increase in the size of a compact *clone* rapidly reduces the P/S ratio while main-

taining an energetically favorable ratio of feeding surface area to volume.

Thoughts on causation: cooperation, kinship, and the link between cloning and aggression

There is an entirely different way to begin thinking about the relationship between cloning and aggression, though it comes to the same thing in the end.

Since the reproductive success of a clone depends on the summed success of its members, a decrease in average *per capita* costs generally increases growth and/or reproductive rates, and increases the fitness of the clone as a whole. However, a behavior that *increases* the costs of a particular individual while causing a greater *total decrease* in the costs (or increase in the benefits) of clonemates would also raise clonal fitness.

The calculus of kinship selection (Hamilton, 1964a, b) was devised specifically to handle this kind of problem. Clonemates are peculiar as kin only because the coefficient of relationship is high and invariant: the fraction of shared alleles is precisely 1.0, or 100%. Among advocates of this approach, it is generally considered good practice to explain phenomena on the basis of individual selection whenever possible, and to invoke kin selection only to explain behavior that consistently *reduces* individual fitness.

In *The Three Musketeers,* Dumas (1844) described reduction of interference costs through *mutual tolerance* and *cooperative association.* Like The Three Musketeers, neighboring clonemates shelter each other from attack on one side. The frequency of aggressive encounters and the individual rate of expenditure on interference will be lower for an individual fighting back-to-back with a clonemate than for a lone fighter of the same size and shape—or more energy can be expended in protecting the exposed sides without increasing total investment. With the same yearly budget for interference, a clonal individual should be able to spend more *per aggressive encounter* than can a single aclonal individual of the same size and shape.

This principle could have broad applicability, since the *necessary* assumptions are few and simple: (1) direct and intense competition with outsiders for some resource, (2) unilateral or reciprocal interference, which is costly both to the initiator and to the recipient, (3) a limited (time/energy) budget for interference, resulting in (4) a (genetically programmed) ceiling on individual investment, and (5) some mechanism for reducing or avoiding interference within the cooperating group.

Kinship within the cooperating group is not necessary. Habituation leading to reduced interference between longterm neighbors (described for *Anthopleura xanthogrammica* by Sebens [1984] and for *Metridium senile* by Purcell and Kitting [1982]) may be examples of *developed tolerance* which decreases interference costs under crowded conditions without sacrificing the ability to discourage newcomers (the dear enemy effect described by Fisher [1954]). *Anthopleura xanthogrammica* is an aclonal, downshore species that lives in very crowded conditions only when it cannot move away from neighbors (Sebens, 1982c). *Metridium senile,* is primarily a resident of the shallow subtidal, where high levels of *interspecific* interference (Sebens, 1985) probably add to its interference costs. It is not yet clear whether these anemones habituate only to contact with members of their own species. The only high shore species tested to date (*Anthopleura elegantissima*) does not seem to habituate at all (N. Withers, cited in Purcell, 1977).

However, cooperation between clonemates *is* unique in being *perfectly stable evolutionarily.* In any other interaction, an individual that can consistently reap the benefits of an association while avoiding attendant costs has a competitive advantage over its purely cooperative neighbor. There is *no* selective advantage to outcompeting a clonemate.

Applied to clonemates, The Three Musketeers analogy can also be formulated as a special case of the energy efficiency model described above. Two additional assumptions are required: (1) Individual size is assumed to be the same for clonal and aclonal genets, and thus individual feeding and metabolic rates can be assumed to be the same. (2) And consequently, clonal genets are assumed to be larger than aclonal genets. These simplifying assumptions probably fit the intertidal anemones well enough to make the model useful for this case. Clones often become very large (Shick and Lamb, 1977; Shick et al., 1979; Sebens, 1982b; Hoffmann, 1986; Fujii, 1987), while individual size in a particular habitat tends to be relatively narrowly constrained by energy considerations (Sebens 1981, 1982a, b) or eventually limited by physiological or mechanical stress.

Since *individual* dimensions are assumed to be constant, clonal feeding surface area is proportional to the number of individuals in a clone.

$$S_c = S_i \cdot n \propto n \tag{7}$$

Therefore the average length of exposed perimeter per individual (P_c/n) is proportional to the ratio of clonal perimeter to clone surface area.

$$P_c/S_c = P_c/S_i \cdot n \propto \ldots \tag{8}$$

Combining Equations 6 and 8 shows that the average length of exposed perimeter per individual and the ratio of clone perimeter to feeding surface area decline at the same rate with increasing clone size.

$$P_c/n \propto P_c/S_c \propto L^{-1} \cdot n^{-0.5} \propto V_i^{-0.33} \cdot n^{-0.5} \tag{9}$$

This version of The Three Musketeers analogy (Equation 9) can be reduced to the simple assertion that as the size of a compact clone increases from one individual (= aclonal genet) to greater than one (= clonal genet), the mean interference cost per individual ($\propto P_c/n$) and the fraction of clonal energy intake required for interference ($\propto P_c/S_c$) should both decline at the same rate (shown as the slope of the lower line in Fig. 3).

For species that produce more dispersed or irregular-shaped clones, *per capita* interference costs will be closer to those of an aclonal individual of the same size.

In species that generally produce small clones, most members are in contact with the external perimeter, so interference costs should tend to be quite evenly distributed. Where *actual* individual costs are approximately the same as the calculated average cost per individual, clone fitness will be maximized when investment in interference maximizes *individual* growth plus reproduction.

By contrast, costs can be very unevenly distributed in large compact clones, because members remote from the edge do not engage in interference, while peripheral members commonly have costs far above the calculated average. In species where this is generally the case, selection should tend to favor an individual investment ceiling that maximizes *clonal* growth and reproduction at the *expense* of the individual reproduction and/or growth of peripheral members. For example, clones of *Anthopleura elegantissima* can be very large (Francis, 1973a; Sebens, 1982b); and peripheral members that invest heavily in interference usually do not produce gametes (Francis, 1976). This could be described as kin selection at the level of the clone.

Thoughts on causation: cloning, body size, and habitat

Upshore/downshore differences in both physical and biological selection pressures can be important in determining appropriate body size and shape for sessile marine invertebrates of various kinds (Connell, 1972, 1975; Paine, 1969, 1976; Denny *et al.*, 1985; Jackson, 1977, 1985), including the sea anemones (Johnson and Shick, 1977; Sebens 1977, 1979, 1980, 1981, 1982a, b, d; Francis, 1979; Harris and Howe, 1979; Minasian, 1979; Shick *et al.*, 1979; Annett and Pierotti, 1984; Elliott *et al.*, 1985; Harris, 1986).

Physical forces caused by breaking waves generally prevent growth to large size on the upper shore (Denny *et al.*, 1985); and large size is not energetically feasible for anemones living upshore, where stress levels are high and feeding is limited to relatively short periods during high water (Sebens, 1982a). And indeed, the larger-bodied species in this sample all live on the lower shore.

Coates and Jackson (1985) argue that because cloning allows increase in biomass for a particular genotype without increase in individual (modular) size, aclonal animals should generally be larger than the component modules of related clonal forms; and they cite the British sea anemones as an example. The data presented here confirm and extend that finding. Individual body size tends to be smaller among the clonal anemone species, which more commonly live upshore.

In exposed microhabitats on the upper shore, clones tend to be closely packed and to present a low, stream-lined profile (Francis, 1973a). During long periods of low tide, this reduces water loss (Roberts, 1941). Underwater and in steady flows, it also reduces the drag forces experienced by the individuals (Koehl, 1977; Denny *et al.*, 1985). Reduction in interference costs is yet another advantage of clonal aggregation. The tendency for clones to remain together may also favor increased mutual dependence through the development of rudimentary chemical communication (Howe and Sheikh, 1975) and division of labor (Francis, 1976). But aggregation is not without its costs. Uncoordinated asexual replication within clonal aggregations will generally result in severe crowding. Where desiccation, water drag, and interference costs are relatively unimportant, clonal *dispersion* may be advantageous in providing more room for growth (McFadden, 1988; D. Stoner, pers. comm.).

Downshore and in protected habitats where it *is* feasible, large individual size can provide advantages, including the ability to eat larger prey (Sebens, 1981), advantage in competitive interactions (Brace and Pavey, 1978) and better resistance to predators (Sebens, 1977 and 1982d; Harris, 1976 and 1986; Elliott *et al.*, 1985). But in spite of the obvious benefits of unlimited growth through asexual replication, none of the large downshore species are also clonal, suggesting that large body size may be mechanically or strategically incompatible with asexual replication for the anemones. (1) Larger individuals seem to heal very slowly after equal, binary fission (pers. obs.). (2) Fragmentation produces repeated and more or less drastic fluctuations in adult body size. This could be hazardous in the presence of predators, which are generally more abundant and diverse downshore (Paine, 1966; Seed, 1969; Jackson, 1985), and typically prefer smaller prey (Brace and Pavey, 1978; Harris and Howe, 1979; Annett and Pierotti, 1984; Harris, 1986). (3) By internal brooding of small, asexual propagules, a large anemone could avoid significant damage and size decrease while offering protection to the growing clonemate; but again, brooding seems to be linked with small body size for marine invertebrates (Strathmann and Strathmann, 1982).

Among the anemones, growth to large individual size and increase in clone size by asexual replication can be seen as alternative growth strategies (Sebens, 1982a).

Taken together, all of this may explain why small-bod-

ied, clonal species are more common high in the rocky intertidal, while large, aclonal anemones are more common near the low water mark. In exposed positions on wave-swept shores, large individual size is physically impractical. However, through asexual replication, a clone can continue to grow while the component individuals remain small. High on the shore, clonal aggregation can provide some protection both from drag forces and from desiccation stress. Downshore, increasing size-selective predation may generally tip the balance in favor of large, aclonal anemones, even though this usually means hiding in pockets and crevices to reduce hydrodynamic forces, and sacrificing the potential for unlimited (clonal) growth.

Thoughts on causation: habitat and aggression

At a coarse level of resolution, there is an obvious relationship between habitat and the evolution of aggression among sea anemones. (1) Aggression is unknown among burrowing anemones on soft substrata. Exclusive use of a living area may only be worth fighting for if it is relatively stable. (2) On hard substrata, no aggressive species yet described is confined to the subtidal. Some aggressive anemones (*e.g., Metridium senile* and *Anthopleura artemisia*) occur both in the subtidal and in the intertidal, but so far as is known, *none* are exclusively subtidal.

Although a higher proportion of upper shore species in the sample are aggressive (9/15 species or 60%, as compared with 3/20 or 15% of the lower shore species), this difference is not statistically significant.

Aggression among brooding anemones

Information on the genetic relationship between parents and brooded offspring exists for only three brooding anemones. Two species of *Actinia* produce asexual broods (Black and Johnson, 1979; Orr *et al.,* 1982); and both are aggressive toward genetically different individuals and tolerant of neighboring clonemates (Ottaway, 1978; Ayre, 1983; Brace, 1981; Brace *et al.,* 1979). One species of *Epiactis* is known to brood sexual offspring produced through self-fertilization (Bucklin *et al.,* 1984).

If self-fertilization (or inbreeding of any sort) is common among brooding anemones, the coefficient of relatedness might be very high between neighboring individuals. Again, this would tend to stabilize cooperative interactions between neighbors, which could make interference with outsiders more feasible economically. It is intriguing to note that although no aggressive behavior has been reported for members of the brooding *Epiactis* species, they have recently been shown to produce holo-

trichs (Fautin and Chia, 1986), a type known to function only in aggression, among the actiniarians.

Generalizing beyond anemones: other anthozoans

Volumes have been written on the biology of clonal organisms (Larwood and Rosen, 1979; Jackson *et al.,* 1985; Harper *et al.,* 1986). While a general review is beyond the scope of this paper, it does seem appropriate to comment on some obvious differences between the patterns described here for rocky shore anemones, and what is known about the relationship of cloning to aggression, body size, and habitat among common and closely related animals such as the corallimorpharian anemones, the scleractinian hard corals and the alcyonarian gorgonians and soft corals.

Clonal anthozoans with small polyps certainly are *not* uncommon in the subtidal. The corallimorphs are typically clonal and subtidal. The corals, gorgonians, and soft corals are typically subtidal and *colonial* forms with relatively small polyps. In fact, Jackson (1985) maintains that with the exception of the sea anemones, clonal animals living on hard substrata are generally more abundant and diverse in deeper water than in shallow water.

One important difference between intertidal anemones and the subtidal anthozoans may be vulnerability to predators. Since predator diversities and abundances tend to increase downshore (Paine, 1966; Seed 1969; Jackson, 1985), exposed and sedentary creatures of the shallow subtidal probably require especially effective defenses (Jackson, 1977). The temperate corallimorphs have exceptionally large nematocysts and seem to be less palatable to their downshore predators than are the local Actiniaria (Annett and Pierotti, 1984). Scleractinians secrete a protective hard skeleton; and soft corals commonly sequester toxic chemicals. Furthermore, among colonial organisms, asexual replication need not involve fluctuations in either polyp or colony size. Among colonial forms, resistance to predators may be as much a function of colony size as of polyp size (Jackson, 1985). Parenthetically, the nematocyst-laden acontia of the worldwide, clonal and aggressive anemone *Metridium senile* may be the secret to its success on the lower shore and in the subtidal, since species without acontia seem to be even more vulnerable to predators than is *M. senile* (predator preference tests by Annette and Pierotti [1984] and Harris [1986]).

More generally, then, cloning may be associated *either* with low predator pressure (*e.g.,* clonal anemones on the high shore), *or* with powerful antipredator defenses (*e.g.,* the large nematocysts of subtidal and clonal corallimorphs).

Another difference between the intertidal anemones and the typically subtidal anthozoans is that while ag-

gressive anemones will attack nonclonemate members of their own species *and* other species of anthozoans, with a few exceptions (Potts, 1976; Hidaka and Yamazato, 1984), aggression among the subtidal forms is exclusively interspecific (Sheppard, 1982; Chadwick, 1987). Allelopathic chemicals released by some soft corals interfere with the growth of hard coral species (Sammarco *et al.,* 1983) and other soft coral species (Coll and Sammarco, 1986). Some scleractinians and corallimorphs digest neighboring competitors of various species (Lang, 1973; Chadwick, 1987). And some hard corals and gorgonians attack neighbors with specialized and inducible sweeper tentacles (Den Hartog, 1977; Richardson *et al.,* 1979; Wellington, 1980; Chornesky, 1983), or with specialized sweeper polyps (Sheppard, 1982). Although histocompatibility reactions often prevent anastomosis where adjacent coral or alcyonarian colonies come into contact with another clone of the same species (Theodor, 1970; Hildemann *et al.,* 1979), this seems to be an example of growth limitation through exploitation competition, rather than interference.

Again this difference may be related to the difference in habitat. Anemones typically confront relatively few competing species in the intertidal (Francis, 1985); and so direct *intraspecific* competition for space is probably more common and important there than in the subtidal. In the shallow subtidal, where patterns of space use are often more mosaic and changeable (Sebens, 1985), interspecific interference can be quite important, both for the anemones that live there (Chao, 1975; Purcell, 1977; Sebens, 1976, 1985; Shick *et al.,* 1979) and for these other subtidal anthozoans.

So far no one has looked for a correlation between cloning and aggression among the common subtidal anthozoans. The geometric analysis developed for the anemones would require appropriate modifications before it could be applied to three dimensional colonies. However the intuitive version of The Three Musketeers analogy again suggests that interference should be less costly, and consequently more commonly affordable, where tolerant neighbors repel other competitors—regardless of whether the competitor is a member of the same species or of some other species, and regardless of whether the tolerant neighbor is a member of the same colony, clone, or species. Since cooperative association between clonemates *is* unique in being completely stable evolutionarily, *interspecific* interference may also tend to be particularly common among massive colonial forms, and among clonal or colonial forms that ramify or fragment to produce relatively large genets.

However, there are two specific provisos: (1) interference must be costly, and (2) association (with clonemates or other species members) must reduce the costs or increase the benefits of interference. If the corals and coral-

limorphs that eat neighboring competitors actually *gain* more energy than they lose in the interaction (Sheppard, 1982), then the principle would *not* apply. For alcyonarians, it is also not clear whether the costs of allelopathy can be reduced or the benefits increased through cooperative association.

Like the acrorhagi and catch tentacles of aggressive anemones, the sweeper tentacles and sweeper polyps of some hard corals and gorgonians appear to be specialized, costly, inducible, and locally effective interference structures. For this kind of interspecific interference, costs probably *are* reduced through association with conspecifics; and I would expect these behaviors to be relatively less costly and thus more common or better developed, among species that produce large colonies or individuals among species that commonly form large genets through some kind of asexual replication, and among species that tend to form monospecific aggregations.

The evolution of social aggression

Social aggression implies cooperation within a group of individuals and interference between groups. Therefore, the circumstances favoring the evolution of these behaviors must include *both* those favoring the evolution of intraspecific cooperation *and* those favoring the evolution of intraspecific interference.

The following circumstances seem to favor the evolution of *intraspecific interference* for all sorts of animals, including sea anemones: (1) longevity (no evidence of programmed senescence among anemones), (2) high densities (caused here by local recruitment and accumulation of long-lived, asexually produced individuals), and (3) competition for a limiting resource (in this case, attachment space and access to food).

Circumstances favoring the evolution of intraspecific *cooperation* within an aggressive species include the following: (1) proximity (commonly caused in the anemones by asexual replication), (2) kinship among neighbors (genetic identity among anemone clonemates), and (3) advantage in cooperation (in this case, increased resistance to physical stress for animals in closely packed aggregations, plus reduction of interference costs).

Additional, specific requirements for the evolution of social aggression include the following: (1) cooperative reduction in interference costs or increase in benefits, and (2) the ability to recognize members of the cooperating group and exempt them from attack.

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